



# How important is it to consider lineage diversification heterogeneity in macroevolutionary studies? Lessons from the lizard family Liolaemidae

## Abstract

Macroevolutionary and biogeographical studies commonly apply multiple models to test state-dependent diversification. These models track the association between states of interest along a phylogeny, although many of them do not consider whether different clades might be evolving under different evolutionary drivers. Yet, they are still commonly applied to empirical studies without careful consideration of possible lineage diversification heterogeneity along the phylogenetic tree. A recent biogeographic study has suggested that orogenic uplift of the southern Andes has acted as a species pump, driving diversification of the lizard family Liolaemidae (307 described species), native to temperate southern South America. Here, we argue against the Andean uplift as main driver of evolution in this group. We show that there is a clear pattern of heterogeneous diversification in the Liolaemidae, which biases state- and environment-dependent analyses in, respectively, the GeoSSE and RPANDA programs. We show here that there are two shifts to accelerated speciation rates involving two clades that have both been classified as having “Andean” distributions. We incorporated the Geographic Hidden-State Speciation and Extinction model (GeoHiSSE) to accommodate unrelated diversification shifts, and also re-analyzed the data in RPANDA program after splitting biologically distinct clades for separate analyses, as well as including a more appropriate set of models. We demonstrate that the “Andean uplift” hypothesis is not supported when the heterogeneous diversification histories among these lizards is considered. We use the Liolaemidae as an ideal system to demonstrate potential risks of ignoring clade-specific differences in diversification patterns in macroevolutionary

studies. We also implemented simulations to show that, in agreement with previous findings, the HiSSE approach can effectively and substantially reduce the level of distribution-dependent models receiving the highest AIC weights in such scenarios. However, we still find a relatively high rate (15%) of distribution-dependent models receiving the highest AIC weights, and provide recommendations related to the set of models included in the analyses that reduce these rates by half. Finally, we demonstrate that trees including clades following different dependent-drivers affect RPANDA analyses by producing different outcomes, ranging from partially correct models to completely misleading results. We provide recommendations for the implementation of both programs.

## 1 | INTRODUCTION

Macroevolutionary modelling of diversification plays an important role in inferring large-scale biodiversity patterns (Schluter, 2016). Several studies have focused on quantifying differences in macroevolutionary patterns linked to geographic, ecological, life history and other traits based on the variation in speciation and extinction rates (Condamine, Rolland, & Morlon, 2013; Jablonski, 2008; Ng & Smith, 2014; Rabosky & McCune, 2010). Given that mechanisms underlying the correlations between characters and diversification are generally poorly understood (Rabosky & Goldberg, 2015), a family of State-Dependent Speciation and Extinction (SSE) models have been developed. The earliest models included binary traits (Maddison, 2006), quantitative traits (FitzJohn, 2010), geographic character states (Goldberg, Lancaster, & Ree, 2011), multiple character states (FitzJohn, 2012), punctuated trait changes (Goldberg & Igic, 2012; Magnuson-Ford & Otto, 2012) and time-dependent

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macroevolutionary rates (Rabosky & Glor, 2010). These models track associations between the states of interest and speciation and extinction rates along a phylogenetic tree, and they have been implemented in hundreds of empirical studies (Rabosky & Goldberg, 2015). In addition, interest has also increased in the application of correlative algorithms (Condamine et al., 2013; Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012; Morlon et al., 2016; Steeman et al., 2009; Winkler et al., 2010), as implemented in the software RPANDA (Morlon et al., 2016), to use environment-dependent models to test whether gradual changes in palaeoenvironments have significantly influenced speciation and extinction rates. These state- and environment-dependent models have become popular, but important concerns have been raised (at least) for the SSE family of models that do not consider whether unrelated traits are associated with shifts in diversification rates (Beaulieu & O'Meara, 2016; Maddison & FitzJohn, 2014; Rabosky & Goldberg, 2015, 2017). For example, strong correlations with diversification are sometimes inferred from rate shifts, leading to dramatically high rates of false positives even if the shift is unrelated to the targeted state (FitzJohn, 2010; Maddison & FitzJohn, 2014; Maddison, Midford, & Otto, 2007; Rabosky & Goldberg, 2015, 2017). These issues may also be affecting environment-dependent correlative models in such scenarios (Lewitus & Morlon, 2018). Consequently, while larger trees are preferred due to the presumed increase in power, this also increases the risk of including clades that differ in factors that can affect diversification rates along a tree (ecological requirements, dispersal abilities, and life history traits [Li, Huang, Sukumaran, & Knowles, 2018]). Hence, at least for the case of SSE models, new algorithms that include "hidden states" (HiSSE) have been proposed for binary traits (BiHiSSE; Beaulieu & O'Meara, 2016), and more recently geographic-dependent diversification hypotheses (GeoHiSSE; Caetano, O'Meara, & Beaulieu, 2018) and multiple states (SecSSE; Herrera-Alsina, Els, & Etienne, 2019). Hidden states refer to unsampled traits that are related to diversification shifts in a phylogenetic tree, thus incorporating heterogeneous diversification into the original SSE.

The HiSSE has improved the SSE model family and potentially resolved the problem of unrelated shifts in the phylogeny when appropriate sets of models are tested (Beaulieu & O'Meara, 2016; Caetano et al., 2018; Herrera-Alsina et al., 2019). On the other hand, there are no currently available solutions for environment-dependent models (i.e. hidden states have not been implemented so far), besides splitting clades into separate analyses (Lewitus, Bittner, Malviya, Bowler, & Morlon, 2018). Even though models that do not include hidden states are not suitable for trees including groups with heterogeneous diversification patterns, they are still commonly applied in macroevolutionary studies without careful assessment. For instance, the Geographic State Speciation and Extinction model (GeoSSE; Goldberg et al., 2011) was recently used in biogeographic studies of lizards (Esquerré, Brennan, Catullo, Torres-Pérez, & Keogh, 2019), tanagers and tortoises (Román-Palacios & Wiens, 2018), plants (Canal et al., 2019),

including palms (Bacon, Velásquez-Puentes, Hoorn, & Antonelli, 2018) and oaks (Hipp et al., 2018), and a recent mega-phylogeny of mushrooms (Varga et al., 2019). Given the above-noted limitations of this model, these empirical cases should be revisited (e.g. Harrington & Reeder, 2017). Here, we re-analyse the recently published phylogeny of the lizard family Liolaemidae (Esquerré et al., 2019), and show how the main conclusion can change when considering heterogeneous diversification in state- and environment-dependent hypotheses tests.

The lizard family Liolaemidae is the most species-rich lizard clade in southern South America (307 species; Reptile Database 11 February 2019). The clade includes three genera: *Ctenoblepharys*, *Liolaemus* and *Phymaturus* (Table 1). *Ctenoblepharys* is a monotypic genus restricted to the coastal desert of Peru (Table 1), whereas *Liolaemus* is the world's richest temperate zone genus of extant amniotes (Olave, Avila, Sites, & Morando, 2018), with 262 described species (Reptile Database 2 February 2019). This clade includes a highly diverse group of species inhabiting a wide range of different environments (Table 1), and the sister genus *Phymaturus* (44 species; Reptile Database 2 February 2019) is distributed along both the eastern and western Andean slopes in Argentina and Chile (*palluma* clade), and through Patagonia (*patagonicus* clade). *Phymaturus* are highly specialized lizards, strictly saxicolous and largely restricted to volcanic plateaus and peaks (Ceí, 1986).

The three genera have clear differences in species richness, ecological requirements, behaviours and life histories (Table 1). A recent macroevolutionary study found disparate patterns of diversification among the three genera (Olave, Gonzalez Marin,

**TABLE 1** Summary of distribution, habitat use, diet and reproductive mode among the three Liolaemidae genera

	<i>Ctenoblepharys</i>	<i>Phymaturus</i>	<i>Liolaemus</i>
Described species	1	44	262
Distribution	Perú	Argentina Chile	Argentina Chile Perú Bolivia southern Brazil Paraguay Uruguay
Habitat	coastal desert	saxicolous	terrestrial arboreal arenicolous saxicolous
Diet	insectivores	herbivores	herbivores omnivores insectivores
Time for sexual maturity	unknown	7–8 years	~2 years
Reproductive mode	oviparous	viviparous	viviparous oviparous parthenogenesis



Avila, Sites, & Morando, in press), whereas another recent biogeographic study focused on the entire clade, overlooking these striking differences between *Phymaturus* and *Liolaemus*, and the diversification rate shifts along the tree (Esquerré et al., 2019). The Esquerré et al. study represents a major contribution to evolutionary biology and herpetology in that it: (a) presents the largest Liolaemidae time-calibrated phylogeny to date (258 taxa), (b) the most extensive compilation of habitats, altitudes, and temperature data for all taxa, and (c) documents shifts in parity modes, including reversals from viviparity to oviparity, a transition believed to be rare. However, Esquerré et al. approach the state-dependent hypothesis using the GeoSSE to test for differences in speciation rates in Andean versus non-Andean (low elevation) species, and detected higher speciation rates in the Andean areas. They also performed correlative environment-dependent analyses in RPANDA programme and found a significant exponential relationship of speciation rate with Andean uplift. Combining these results with ancestral area reconstructions, the authors infer that the Andean orogeny has acted as a “species pump” and that it is the main driver of diversification in the evolution of Liolaemidae.

Here, we show that clade-specific differences within the Liolaemidae have affected the conclusions drawn from GeoSSE and RPANDA. We re-analysed this dataset and show that Andean uplift dependency is not supported as the main driver of Liolaemidae diversification, when considering heterogeneous diversification across the clade's phylogenetic history. In this study, we (i) present an alternative explanation to Esquerré et al., to describe the diversification patterns within the Liolaemidae; and (ii) based on simulation studies, suggest recommendations that should be considered in empirical studies using the state- (HiSSE) and environment-dependent (RPANDA) models.

## 2 | MATERIALS AND METHODS

Here, we briefly describe our methods, but for further details, see the Extended Materials and Methods in the Data S1.

### 2.1 | Identifying possible diversification shifts along the tree and exploration of the relationship between speciation rates versus altitude

We explored the association between speciation (and extinction) rates with the maximum altitude of occurrence known for any species (phylogenetic tree and altitude data taken from Esquerré et al., 2019). The phylogenetic tree includes the monotypic *Ctenoblepharys*, 188 described + 11 undescribed species of *Liolaemus*, and 35 described + 23 undescribed species of *Phymaturus* (73% species coverage of all recognized Liolaemidae). We estimated speciation and extinction rates using BAMM 2.5 (Rabosky et al., 2014) because the method estimates rates per

branch, allowing us to compare changes in these rates among the clades and species (i.e. tips) of interest. We also compared BAMM results with the recently introduced ClaDS program (Maliot, Hartig, & Morlon, 2019).

### 2.2 | Hypothesis testing: role of the Andean orogeny in diversification of the Liolaemidae

#### 2.2.1 | Geographic Hidden-State Speciation and Extinction (GeoHiSSE)

We then implemented the GeoHiSSE model (Caetano et al., 2018) using the *hisse* package (Beaulieu & O'Meara, 2016). Given that we do not fully agree with the original classification of Andean and non-Andean species by Esquerré et al. (2019), here we propose an alternative classification, and performed these analyses using both (Table S8). As an example, the “Patagonia” group is distributed across a huge area that was assumed to be “Andean” in Esquerré et al. (2019), which we consider a poor classification for many species. For example, both the *P. patagonicus* and the *L. lineomaculatus* clades are restricted mainly to the lowland Patagonian steppe. In general, the Esquerré et al. (here after the “original classification”) classification recognizes 194 Andean species, 39 non-Andean species and 25 widespread species; here, our preferred classification includes 118 Andean species, 121 non-Andean species and 19 widespread species. We first evaluated the set of 35 different models proposed by Caetano et al. (2018), and performed simulations based on 200 random permutations of geographic distributions (Rabosky & Golberg, 2015) to assess power (for details in simulations see Extended Materials and Methods). Permutations were performed by keeping the Liolaemidae phylogenetic tree, thus maintaining the complexity of the empirical scenario. This strategy allows us to assess the expected rate of distribution-dependent models receiving the highest AIC weights given the specific phylogeny of Liolaemidae. We performed all simulations twice, based on the original and our preferred geographic classification. The models include a wide range of possible scenarios, including 25 area-independent models (CID) indicating no relationship between diversification rates and geographic areas, and 10 area-dependent diversification models (all models listed in Table S7). Given the relatively high rates distribution-dependent models receiving the highest AIC weights found in our simulations (see results), and issues of overparametrization (Caetano et al., 2018), we removed some of the models from the original 35. Specifically, as some of the proposed state-dependent models have a greater number of free parameters than the most complex null models that *hisse* can currently implement (15 free parameters in the most complex CID model [M11 and M17, both including 5 hidden classes]), we suggest that excluding models with > 15 free parameters is important to reduce these rates. Thus, we consider only 32 models, excluding the most complex models (M10, M16 and M32, with 19, 21 and 17 free parameters respectively).

## 2.2.2 | Correlative environment-dependent models in RPANDA

Esquerré et al. tested whether speciation and extinction rates are correlated with the Andean uplift using the R package RPANDA (Morlon et al., 2016). Similar to the description above, they implemented this model on the complete phylogeny of Liolaemidae and did not analyse the two different genera into separate analyses. They fitted a total of 10 models, including eight for Andean uplift dependency versus two null models where rates are constant through time. We believe that this set of models is lacking in alternative scenarios, and that Andean uplift dependency could have been selected simply because null constant rate models are unrealistic. Specifically, the study fails to include time-dependent models (see Lewitus & Morlon, 2018; Morlon, Parsons, & Plotkin, 2011). Time-dependent models represent scenarios of rates changing in time (not constant), but not associated with a specific environmental variable. Thus, here we corrected this analysis in two ways: (a) we separated *Phymaturus* and *Liolaemus* clades for independent analyses because RPANDA does not consider possible rate shifts along the phylogeny, or potentially different rates across clades; and (b) we expanded comparisons among a total of 42 models (details in Table S9), including time dependency, as well as an alternative environmental variable based on global temperature variation during the past 67 mya (Condamine et al., 2013; original data from Zachos, Pagani, Sloan, Thomas, & Billups, 2001; Zachos, Dickens, & Zeebe, 2008). Ambient temperature is an important environmental parameter in reptiles, given that they are ectotherms. These additional models provide a wider range of alternative scenarios beyond simply constant rates, as we incorporated other alternatives into Andean uplift dependency beyond a simple null constant model. See extended Materials and Methods and Table S9 in Data S1 for further details about these analyses.

Given that our empirical results suggest that *Liolaemus* and *Phymaturus* have different diversification drivers (see results), and the fact that RPANDA is not designed to deal with such scenarios, we conducted a simulation study to explore the impact of ignoring such conditions. Here, we wanted to explore the possible outcomes of RPANDA when large trees include clades influenced by different evolutionary drivers. Given that the programme is not designed to deal with such scenarios, it is interesting to know whether: (a) the two true models receive the highest AIC weights, (b) only one true model receives the highest AIC weights or (c) other unrelated models are supported by high AIC weights. We simulated a total of 100 replicated trees under a pure birth model for two different clades (C1 and C2), where the C1 speciation rate is exponentially correlated with temperature ( $\lambda = 0.2$ ;  $\alpha = -0.05$ ) and C2 diversification was influenced as follows:

- (a) C2 with constant speciation rate ( $\lambda = 0.12$ );
- (b) C2 under time-dependent exponentially correlated speciation rate ( $\lambda = 0.2$ ,  $\alpha = -0.025$ );
- (c) C2 under Andean uplift-dependent exponentially correlated speciation rate ( $\lambda = 0.045$ ,  $\alpha = 0.0005$ );

Parameter values used for simulations were selected to produce approximately similar tip numbers between C1 and C2 (average ~ 220–250 each). Both C1 and C2 are set to be 40 mya old.

## 3 | RESULTS AND DISCUSSION

See also extended results in Data S1.

### 3.1 | Disparate patterns of diversification in the lizard family Liolaemidae: further analyses contradict previous study by Esquerré et al. (2019)

#### 3.1.1 | Heterogeneous diversification within the lizard family Liolaemidae

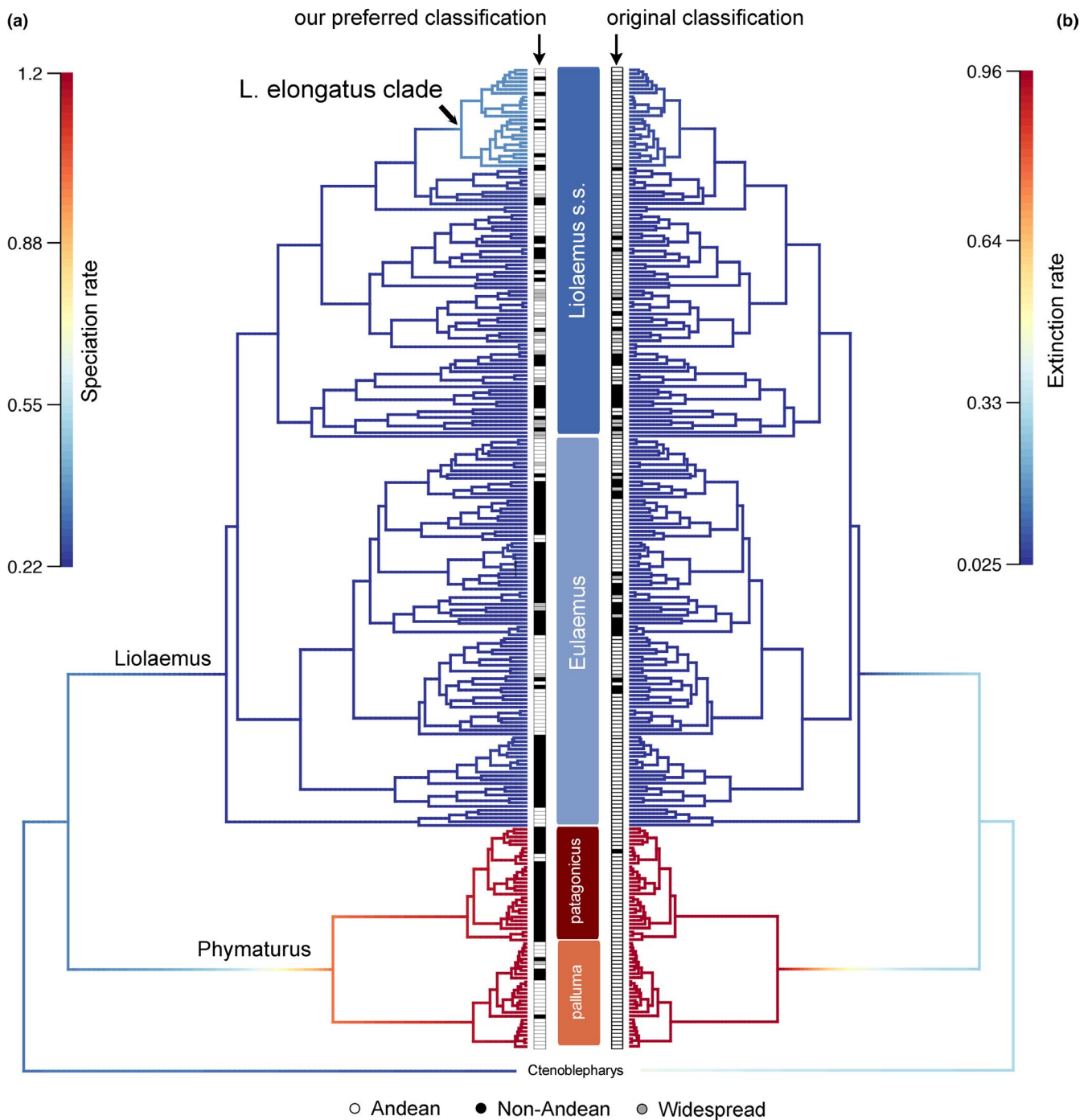
BAMM estimation of speciation and extinction rates in the Liolaemidae phylogeny (Figure 1) displays two shifts (PP = 0.4; Table S2), including the origin of the genus *Phymaturus* (red) and the *Liolaemus elongatus* clade (light blue). There are significant differences in speciation and extinction rates between genera ( $p < .001$ ), as clearly shown by the distributions of parameter estimations (Figure S3; further comparisons within *Liolaemus* shown in Figure S4). Specifically, the genus *Phymaturus* has the highest speciation rate that is also associated with a high extinction rate. This result is concordant with another study using a different phylogenetic tree (Olave et al., in press), and also supported by similar results recovered using ClaDS (Figure S2). We note that both programmes find two shifts to accelerated speciation rates involving clades that were classified entirely as “Andean” by Esquerré et al. (Table 2).

#### 3.1.2 | Exploration of the relationship between speciation and extinction rates versus maximum altitude

We constructed linear models between the maximum altitude (MA) of species occurrence records, and the species-specific speciation and extinction rates. Linear models reveal non-significant correlations of the speciation/extinction rates with the MA for all target clades (Table S5). Scatter plots show no relationship between rates and MA (Figure 2; Figures S5–S11).

#### 3.1.3 | Incorporating heterogeneous diversification: GeoHiSSE results

Speciation and extinction rate estimates generated by GeoHiSSE are highly congruent with BAMM and ClaDS estimates (Table S3), with higher rates in *Phymaturus* than *Liolaemus* (Figures 1, 3, S2, S13). Note that GeoHiSSE model selection was different when considering the



**FIGURE 1** Color-coded phylogenetic trees for the speciation (a) and extinction (b) rates through time for the Liolaemidae inferred by BAMM. Our preferred geographic classification of species is shown on the left tree and the original geographic classification on the right tree; corresponding to Andean, non-Andean and widespread, shown at each tip in white, black and grey respectively. See Figure S1 for diversification rates

two classifications (Table S7). Following our preferred classification (Figure 3a), the M6 (CID – GeoHiSSE, two hidden rate classes) was associated with the greatest AIC weight ( $=0.5$ ), followed by M12 (CID – GeoHiSSE extirpation, two hidden rate classes; AIC weight = 0.29). Other CID models showed lower support (M3, M19, M9, M20, M5 and M11; Figure 3a; Table S7). On the other hand, results based on the original geographic classification by Esquerré et al. (Figure 3b; Table S7), the M3 (CID – GeoHiSSE, three hidden rate classes) are

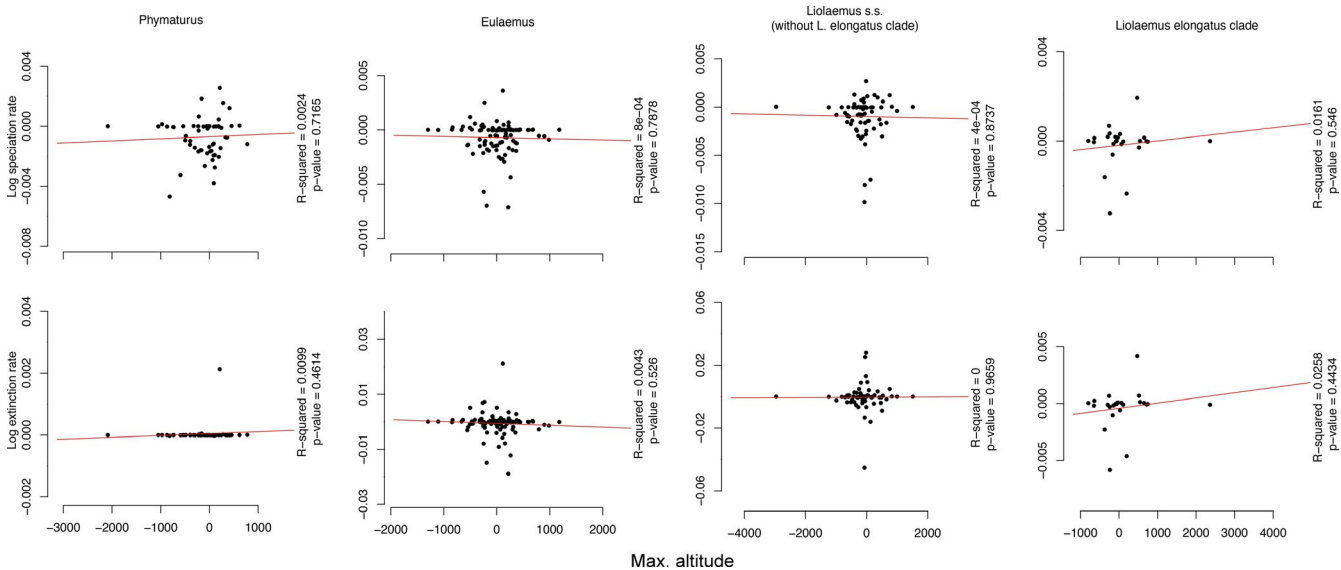
associated with the highest weight ( $=0.47$ ), followed by M18 (CID – anagenetic GeoHiSSE, two hidden rate classes; weight = 0.22) and M19 (CID – GeoHiSSE, four rate classes; weight = 0.17). Other models received little support (weight  $<0.05$ ; M4, M5, M6, M9, M15 and M20).

We have demonstrated that the genera *Phymaturus* and *Liolaemus* display clear disparate patterns of diversification with two clear shifts along the phylogeny (Figures 1, 3 and S2) and that, when



**TABLE 2** Species counts for the geographic classification from Esquerré et al. (2019); taken from their Data S1. Note that some species were classified as both Andean and non-Andean as “widespread” (classification details in Table S8)

	Considered “Andean species”			Considered “Non-Andean species”		
	Patagonia	Central andes	Altiplanic andes	Central chile	Atacama desert	Eastern lowlands
<i>Liolaemus</i>	63	48	56	17	14	32
<i>Phymaturus</i>	33	23	5	0	0	1
<i>Ctenoblepharys</i>	0	0	0	0	1	0



**FIGURE 2** Phylogenetically controlled linear regressions of the log-transformed speciation/extinction rates as a function of the maximum altitude of the species occurrence, for different target clades: *Phymaturus* genus, *Eulaemus* subgenus, *Liolaemus* sensu stricto (s.s.) subgenus when excluding the *L. elongatus* clade, and with the *L. elongatus* clade. See also the Figures S5–S11 for more regressions, and Table S5 for full results of the linear models

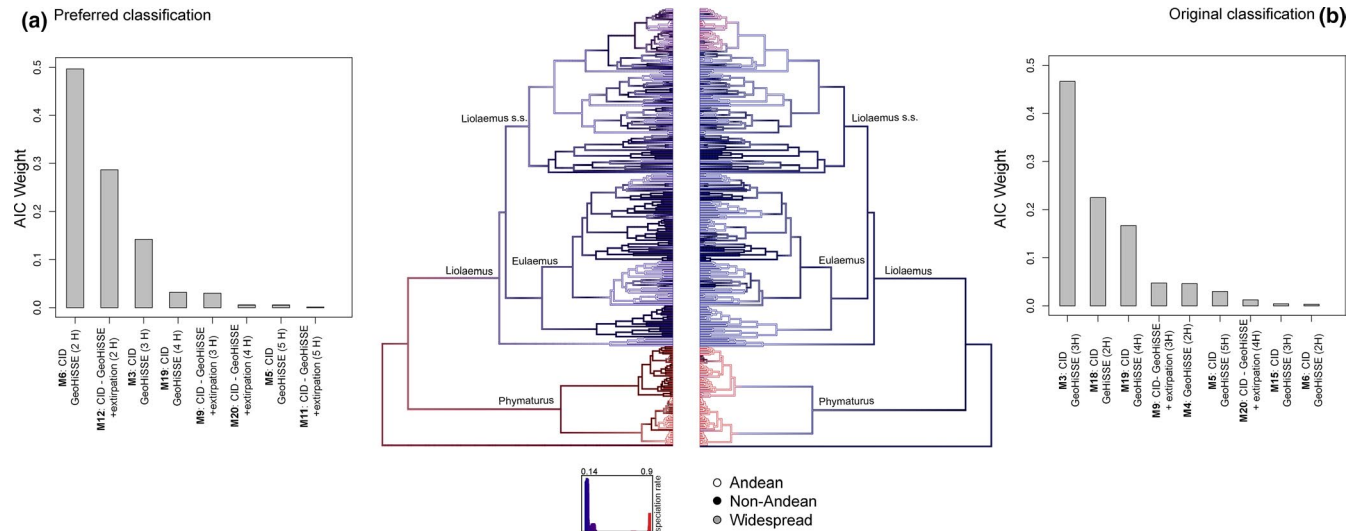
incorporating the HiSSE into the models, results show no apparent signal of Andean uplift increasing speciation rates in the Liolaemidae (Figure 3; Table S7). This is true in both cases, when considering either our preferred geographic classification or the original classification (Figure 3; Table S7). These results show that Esquerré et al. have confounded clade-specific rate accelerations in their distribution-dependent diversification results.

In addition, the GeoHiSSE analyses also return estimates of ancestral distributions (white–black colour gradient in phylogenetic trees in Figure 3). Given the fact that we have changed the geographic classification, these results show that our preferred classification contradicts previous findings by Esquerré et al., using BioGeoBEARS (Matzke, 2016) for ancestral reconstructions. This program returned results showing that ancestral lineages in main clades of Liolaemidae were predominantly Andean, leading Esquerré et al. to conclude that the Andes have acted as a “species pump”, and reinforced the idea that Andean uplift has been a key driver in Liolaemidae diversification. In comparison, our preferred classification now shows that the ancestral *Liolaemus* was most likely “widespread” (i.e., both Andean and non-Andean), and that *Phymaturus* is inferred to have a non-Andean ancestor (Figure 3a). The ancestors of the other subgenera are also inferred to be non-Andean or

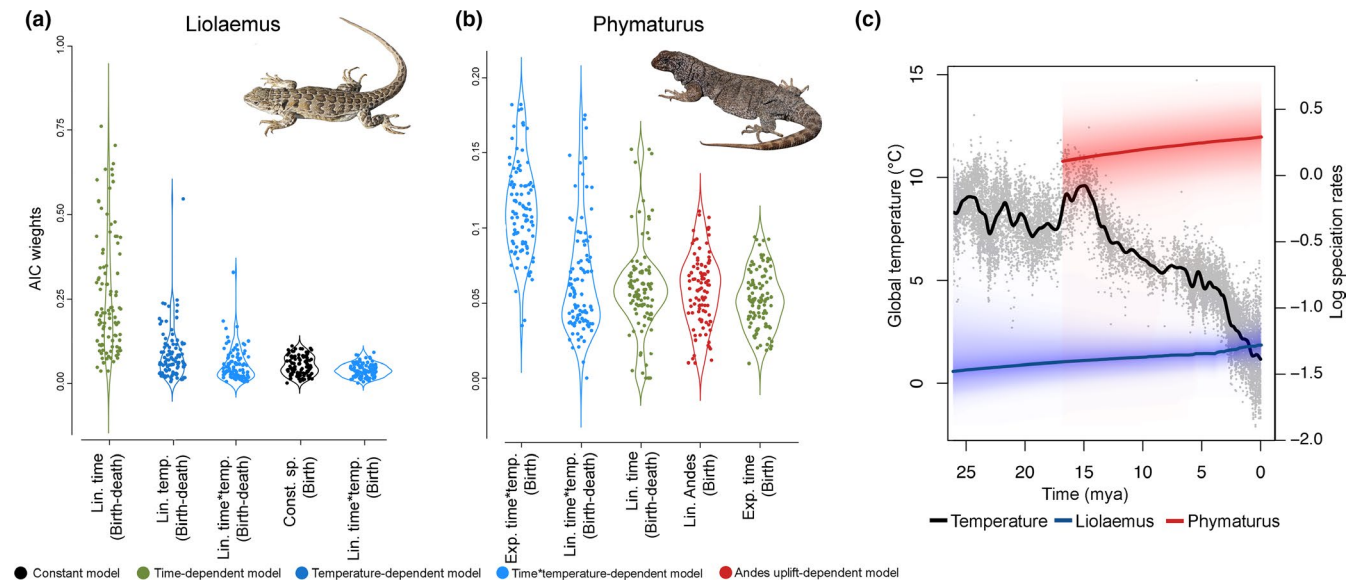
widespread (*Eulaemus*: widespread, *Liolaemus* s.s.: widespread, *P. palluma*: widespread; and *P. patagonicus*: non-Andean; Figure 3a). These results also argue against the Andes acting as “species pump”.

3.1.4 | Correlative environment-dependent models in RPANDA applied to study the lizard family Liolaemidae

We fitted 42 models to each genus within Liolaemidae using RPANDA. This algorithm does not incorporate “hidden states”, so the only proper way to approach such heterogeneous scenarios is by running separate analyses for each genus (but see extended results in Data S1 and Table S9 for analyses of Liolaemidae as a whole). The best model to describe evolutionary rates in *Liolaemus* is a birth–death model in which speciation and extinction rates are linearly correlated with time (i.e. our model 18; Table S9; Figure 4a). This model received an AIC weight average of  $0.26 \pm 0.17$  ( $\lambda = 0.098$ ,  $\alpha = 0.14$ ; Table S9) among 100 trees sampled from the posterior, followed by a model in which speciation and extinction rates are linearly correlated with global temperature changes (AIC weight mean =  $0.08 \pm 0.07$ ; model 15; see Table S9



**FIGURE 3** GeoHiSSE results based on (a) our preferred classification and (b) the original classification. Histograms represent the AIC weights of models fitted to the empirical dataset. Colour-coded phylogenetic tree reflecting the speciation rates (blue-red scale) and geographic states (white-black scale) obtained after averaging parameters of the GeoHiSSE analyses. See Table S7 for further result details



**FIGURE 4** (a,b) Top 5 models (highest AIC weight means) estimated by RPANDA among 42 models for (a) *Liolaemus* and (b) *Phymaturus*. Dots represent AIC weights obtained for 100 different trees sampled from the posterior. All detailed results are presented in Table S9. (c) Global temperature changes through time (grey dots) and a smooth spline in black. Speciation rates estimated by BAMM were log transformed for *Liolaemus* (blue) and *Phymaturus* (red). Temperature data are taken from (Condamine et al., 2013; original data from Zachos 2001)

for details of other models that received little support). In contrast, the best model to describe evolutionary rates in *Phymaturus* corresponds to speciation rates exponentially correlated with the interaction between time and global temperature changes (model 19; AIC weight mean =  $0.11 \pm 0.03$ ;  $\lambda = 1.03$ ,  $\alpha = -0.6$ ; Figure 4b), followed by another model including an exponential dependency of the interaction between time and global temperature changes (AIC weight mean =  $0.06 \pm 0.04$ ; model 25). In addition, other models received support and a higher dispersion of estimated AIC weights, reflecting increased uncertainty in *Phymaturus* relative to *Liolaemus*.

### 3.1.5 | Disparate patterns of diversification in the lizard family Liolaemidae

Interestingly, even though *Liolaemus* has extraordinary species richness (262 described species), our analyses show that its sister group *Phymaturus* evolved under higher speciation rates (44 described species + 23 candidate species included here). Increased speciation rates in *Phymaturus* are best explained by decreasing global temperatures (Figure 4b). Previous studies have shown that the thermal biology of the cold-adapted *Phymaturus* genus

is remarkably similar across species, suggesting that it may be evolutionarily or ecologically constrained (Cruz et al., 2009; Ibargüengoytia et al., 2008). Thus, it is biologically plausible that once the temperature conditions became more favourable for this group, then *Phymaturus*' speciation rates increased (Figure 4b,c). Different abiotic factors have been suggested to affect South American climates, including Andean uplift as one of the possible promoters (e.g. Blisniuk et al., 2006; Gregory-Wodzicki, 2000). Is it possible that the Andes uplift has indirectly driven the increase in speciation rates in *Phymaturus* by promoting local climate change? There has been considerable debate over the role of the Andes relative to South American climate change, including whether the Andes promoted climate change, or global climate change promoted the Andean uplift (Lamb & Davis, 2003). However, post-Cenozoic temperature decrease was a global phenomenon (Zachos et al., 2008; 2001), and a combination of relevant factors also acted as locally cooling promoters, such as the Humboldt Current generated by the closure of the Central America Seaway (Garreaud, Molina, & Farias, 2010; Hartley, 2003). We emphasize that multiple factors have likely driven *Phymaturus* evolution, and assuming a temperature-only dependent diversification is unnecessarily reductionist. We also cannot discard other important aspects in the peculiar biology of this genus. For example, all >40 cold-adapted species only occur in isolated patches of rock outcrops; therefore, migration between populations is likely severely limited relative to *Liolaemus* (Vicenzi, Corbalán, Miles, Sinervo, & Ibargüengoytia, 2017). The strong fidelity of *Phymaturus* species to specific microhabitats, "islands" of big boulders with deep crevices in volcanic cliffs, peaks and plateaus (Ceí, 1986), might have promoted speciation over short periods of time, as is the case in other lizard species in both wild and urban populations (e.g. Templeton, Robertson, Brisson, & Strasburg, 2001; Thompson, Rieseberg, & Schluter, 2018).

Specialization in *Phymaturus* has been discussed in other studies (e.g. Marín-Gonzalez, Olave, Avila, Sites, & Morando, 2018; Olave et al., in press; Reaney, Saldarriaga-Córdoba, & Pincheira-Donoso, 2018); specialization may be advantageous if it results in efficient selection for adaptation to a stable and narrow niche, reducing the cost of trade-offs by abandoning traits needed to utilize a wider range of resources (Futuyma & Moreno, 1988). However, these shorter-term microevolutionary benefits may come at the cost of longer-term macroevolutionary success (e.g. Agnarsson, Avilés, Coddington, & Maddison, 2006; Anacker, Whittall, Goldberg, & Harrison, 2011; Armbruster, 2014; Forister, Dyer, Singer, Stireman, & Lill, 2012). Thus, it is possible that the same factors promoting speciation in *Phymaturus* might also explain its high extinction rates as a trade-off (Figure 1 and S3). The contrasting biology between the sister groups *Liolaemus* and *Phymaturus* (Table 1) makes the Liolaemidae an extraordinarily rich clade in which to explore the cost-benefits of lineages becoming generalists versus specialists, and their roles shaping macroevolutionary dynamics (Olave et al., in press).

### 3.2 | The importance of considering lineage diversification heterogeneity in macroevolutionary studies: warnings in implementation of GeoHiSSE and RPANDA programs

#### 3.2.1 | Assessing the power of GeoHiSSE models: are hidden states improving state-dependent diversification models?

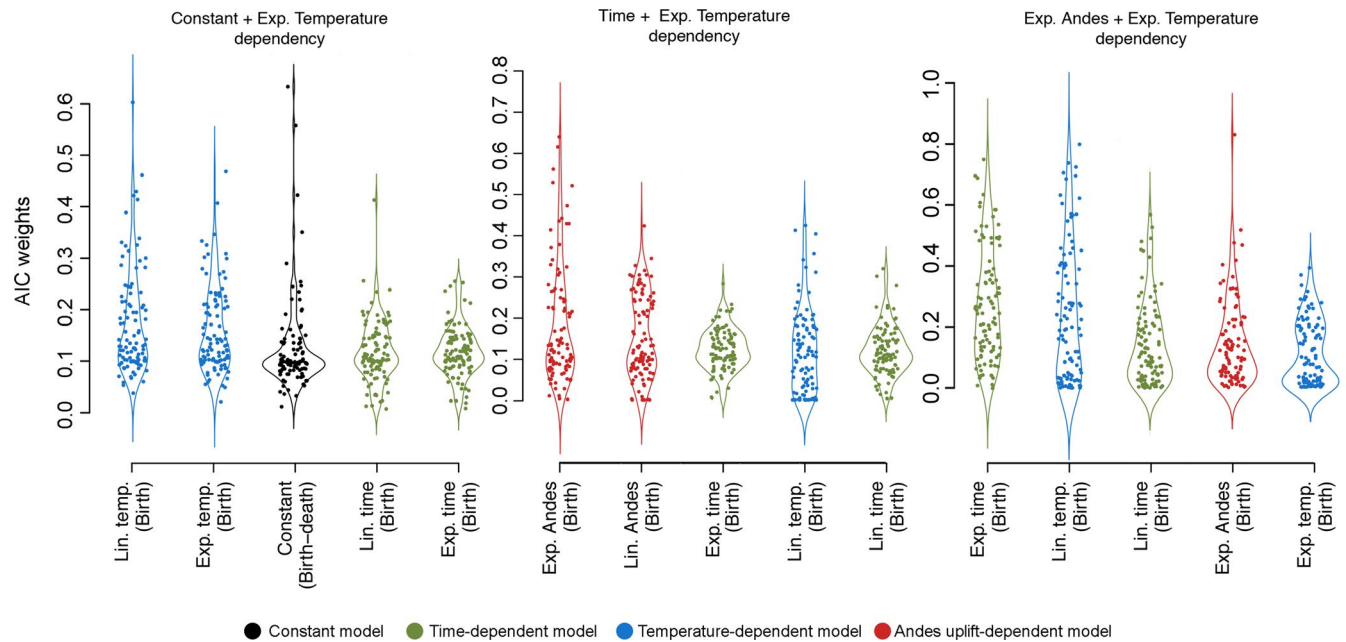
Previously, it has been shown that including hidden states to the model is a plausible solution to account for diversification heterogeneity and improve the accuracy of the original SSE models (Caetano et al., 2018). We assessed the power of GeoHiSSE analyses by simulating random permutations of geographic areas, and show that most of the CID models received the highest weights over distribution-dependent models (~85%). This is undoubtedly an improvement over the high level of false positives reported for the original SSE models (Rabosky & Goldberg, 2015, 2017). However, we still found a relatively high rate of distribution-dependent models receiving the highest weights (=15%) when considering all 35 models and permutations based on the original geographic classifications (Figure S14a; Table S7), and 16% with simulations based on our preferred classification (Table S7). Interestingly, all state-dependent models receiving the highest weights are equal or greater than the maximum number of free parameters (=15 – 21) in the most complex CID model (M11 and M17). Furthermore, most of these models are supported by high AIC weights (Figure S14b). We show that excluding models with >15 free parameters (i.e. selection among 32 models) reduced these rates to 7% (Figure S14c) following the original classification, and to a ~ 10% rate given the permutations on our preferred classification (Table S7; see also extended results in Data S1 for further details).

Given the recent documentation that a proper set of state-independent models for HiSSE methods should, necessarily, have the same number of free diversification parameters than the state-dependent models for a "fair" comparison (Caetano et al., 2018), we think that the original set of 35 models should be taken with caution. This issue was paradoxically shown in Caetano et al. (2018) for BiHiSSE implementation, but not corrected among the 35 proposed models for GeoHiSSE in the same paper. Our study does not mean that the same power estimations will necessarily apply to another empirical phylogeny, but we have demonstrated the importance of assessing power before applying HiSSE models, as well as reinforced the notion of potential risks related to the set of models (and number of free parameters) implemented for HiSSE hypothesis tests.

#### 3.2.2 | Impact of heterogeneous trees in RPANDA: trees including clades following different dependent-drivers affect results

Inspired in our empirical results, we performed a simulation study to address how RPANDA analyses could be affected when two





**FIGURE 5** AIC weight obtained for the simulation studies including heterogeneous scenarios analysed in RPANDA program. Top 5 models (highest AIC weight means) are shown for the different simulated scenarios, including trees comprising one clade (C1) evolving under temperature dependency plus a second clade (C2) evolving either (i) under constant speciation rates (left), (ii) with speciation rates exponentially correlated with time (middle) and (iii) with speciation rates exponentially correlated with the Andes uplift as a second environmental variable (right). Further results are shown in Table S10

different clades in a phylogenetic tree evolve following different drivers. An extensive simulation study to test the performance of RPANDA was performed by Lewitus and Morlon (2018), including exploration of different proportions of missing tips, accurate model selection and also rate shifts along the phylogeny. Although the authors show that RPANDA seem to be robust when rate shifts are present along the phylogeny under their simulated conditions, here we focused on a different type of heterogeneous scenario.

Our results show that, even though RPANDA can accurately recover the true scenario when there is a single driver for speciation rates in a phylogenetic tree (Figure S15; Table S10), there is a range of different outcomes when each clade evolves in response to different drivers of diversification, including selecting partially correct models to completely misleading results (Figure 5). On the one hand, in a scenario where one clade follows a temperature-dependent evolution, while the other clade has constant rates (Figure 5, left; Table S10), the models with highest AIC weights are two temperature-dependent models (model 4 and 2; model 2 is a true model), followed by a constant rate model (model 1; also a true model). Here, recovering the true models with high support might represent the best possible outcome. However, our second set of simulations included a temperature-dependent + time-dependent trees, and the best-supported models are two unrelated Andean uplift-dependent scenarios (model 2b and 4b; Figure 5, middle; Table S10). Further, our 3rd set of simulations included trees evolving following two different environmental variables (temperature + Andean uplift; Figure 5,

right; Table S10), and also returns the highest support for an unrelated model (time dependent; model 3), followed by a temperature-dependent model (model 4; however, not the true model).

Our results highlight clear potential risks of ignoring such heterogeneous diversification histories in RPANDA. Currently, the only way to circumvent such an issue is to recognize potential differences a priori, and separate clades into different analyses. However, while hidden states are not incorporated into RPANDA, it is clearly difficult in practice to recognize which clades should be separated, as identifying speciation rate shifts might not be sufficient. Specifically, two clades with similar rates might follow different environmental drivers. Thus, recognizing clades with important biological differences is key to assess potential differences a priori. As we have shown here, the two contrasting groups of *Liolaemus* and *Phymaturus* not only differ in speciation rates but also in several aspects of their biology (Table 1). Such biological differences are expected to affect the macroevolutionary patterns (Li et al., 2018). Empirical studies must explore such possibilities when using models that do not allow heterogeneous trees, as is the case of the current version of RPANDA.

## 4 | CONCLUSIONS

Incorporating large trees for macroevolutionary studies has the advantage of providing larger datasets, and presumably more power. However, it is important to keep in mind the value of

incorporating heterogeneous diversification rates into models for state- and environment-dependent hypothesis testing. We disagree with the main conclusion of Esquerré et al. that the Andes uplift was the main driver of the diversification of these lizards, by showing that: (a) there is no support for increased speciation rate in Andean species (Figure 3 and Figure S7), (b) a time-dependent model better explains diversification of the genus *Liolaemus* than Andean uplift (Figure 4; Table S9) and (c) a model considering the interaction between time and global temperature changes is a better fit for the genus *Phymaturus* than Andean uplift (Figure 4; Table S9). As a final remark, our preferred classification of species distributions has now changed inferences in ancestral-range reconstructions, and suggests that ancestors of both genera and all four subgenera were non-Andean or widespread (i.e. both Andean and non-Andean; Figure 3a), thus, challenging the Andean “species pump” hypothesis. However, we do not attempt to invalidate the whole work presented by Esquerré et al. As mentioned before, they have presented many other relevant findings about the diversification history of Liolaemidae.

Finally, our study calls attention to the importance of considering heterogeneous diversification when implementing state- and environment-dependent hypotheses tests. Specifically, we have demonstrated that trees including clades following different dependent drivers affect RPANDA results (Figure 5), and the only way to circumvent such problem is to separate clades for independent analyses, given that this method does not account for hidden states. We also provide recommendations for the implementation of GeoHiSSE models to account for fair comparisons among models included in the analysis. We reinforce the previously known case of removing the distribution-dependent overparameterized models in GeoHiSSE (Figure S14; Table S7), to prevent exceeding the number of free parameters in the most complex null model.

We note that, although here we focused on the recently published Liolaemidae phylogeny as a model system, it is very likely that many earlier empirical studies may have limitations similar to those we report here, and these should be re-assessed.

## KEYWORDS

Andes, biogeography, extinction, GeoHiSSE, GeoSSE, hidden states, macroevolution, RPANDA, speciation

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## DATA AVAILABILITY STATEMENT

The data to support the findings of this study will be openly available in the DRYAD Digital Repository: <https://doi.org/10.5061/dryad.kd51c5b2c>.

Melisa Olave<sup>1,2</sup> 

Luciano J. Avila<sup>3</sup>

Jack W. Sites<sup>4</sup>

Mariana Morando<sup>3,5</sup>

<sup>1</sup>Department of Biology, University of Konstanz, Konstanz, Germany

<sup>2</sup>Instituto Argentino de Investigaciones de Zonas Áridas, Consejo Nacional de Investigaciones Científicas y Técnicas (IADIZA-CONICET), Mendoza, Argentina

<sup>3</sup>Instituto Patagónico para el Estudio de los Ecosistemas Continentales, Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Argentina

<sup>4</sup>Department of Biology and M.L. Bean Life Science Museum, Brigham Young University (BYU), Provo, UT, USA

<sup>5</sup>Universidad Nacional de la Patagonia San Juan Bosco, Sede Puerto Madryn, Puerto Madryn, Argentina

## Present address

Jack W. Sites, Department of Biology, Austin Peay State University, Clarksville, Tennessee, USA

## Correspondence

Melisa Olave, Department of Biology, University of Konstanz, Konstanz, Germany.  
Email: [melisa.olave@uni-konstanz.de](mailto:melisa.olave@uni-konstanz.de)

## ORCID

Melisa Olave  <https://orcid.org/0000-0002-7773-0189>

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### BIOSKETCH

Melisa Olave is an Alexander von Humboldt postdoctoral researcher at the University of Konstanz (Germany) interested in phylogenetics, phylogeography and biogeography fields. Her research aims to look into how physical and biological factors influence gene flow and lineage diversification, and ultimately speciation and extinction.

### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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